Attention modulates visual size adaptation

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The current study determined in healthy subjects ($n = 16$) whether size adaptation occurs at early, i.e., preattentive, levels of processing or whether higher cognitive processes such as attention can modulate the illusion. To investigate this issue, bottom-up stimulation was kept constant across conditions by using a single adaptation display containing both small and large adapter stimuli. Subjects' attention was directed to either the large or small adapter stimulus by means of a luminance detection task. When attention was directed toward the small as compared to the large adapter, the perceived size of the subsequent target was significantly increased. Data suggest that different size adaptation effects can be induced by one and the same stimulus depending on the current allocation of attention. This indicates that size adaptation is subject to attentional modulation. These findings are in line with previous research showing that transient as well as sustained attention modulates visual features, such as contrast sensitivity and spatial frequency, and influences adaptation in other contexts, such as motion adaptation (Alais & Blake, 1999; Lankheet & Verstraten, 1995). Based on a recently suggested model (Pooresmaeili, Arrighi, Biagi, & Morrone, 2013), according to which perceptual adaptation is based on local excitation and inhibition in V1, we conclude that guiding attention can boost these local processes in one or the other direction by increasing the weight of the attended adapter. In sum, perceptual adaptation, although reflected in changes of neural activity at early levels (as shown in the aforementioned study), is nevertheless subject to higher-order modulation.

Introduction

Information processing within our sensory systems is highly flexible. The neural responses to sensory stimulation not only depend on the stimulus itself but also on the actual state of the system that changes every moment and with every bit of information processing. This flexibility is illustrated by the phenomenon of adaptation. Adaptation refers to a sensory system's tendency to adjust neural responsiveness after prolonged exposure to a particular sensory stimulation. This tendency represents a general principle of sensory processing and can be observed across different sensory systems, e.g., in visual adaptation (e.g., review by Kohn, 2007), auditory fatigue (Dix, Hallpike, & Hood, 1949; Westerman & Smith, 1984), and vibro-tactile adaptation (Cohen & Lindley, 1938; O'Mara, Rowe, & Tarvin, 1988). Sensory adaptation has marked effects on how we perceive the world. For instance, the perceived size of a target is upscaled after prolonged presentation of a similar stimulus at notably smaller size and, vice versa, downscaled after prolonged presentation of a similar stimulus at notably larger size. This process is referred to as size adaptation. Similar to other size illusions, size adaptation alters

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the eccentricity of primary visual cortex (V1) activation, suggesting that this particular type of adaptation originates within V1 (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006; Pooresmaeili, Arrighi, Biagi, & Morrone, 2013; Schwarzkopf, Song, & Rees, 2011; Sperandio, Chouinard, & Goodale, 2012). Pooresmaeili et al. (2013) found a correlation between the illusionary size changes and the activation within V1 and explained the illusion by local processes in V1, presumably triggered by the contours of the adapter. Although these data emphasize an important role of early visual areas in size adaptation, they cannot resolve the question of whether the effects observed in these regions emerge solely from feed-forward processes or may be generated via feedback processes from higher cortical regions (Chouinard & Ivanowich, 2014). In terms of a theoretical distinction, the question arises of whether size adaptation is mainly determined by stimulus properties without any or with only minor influence from endogenous and top-down settings. For instance, attention could change size adaptation along with size perception. In fact, attention has previously been shown to modulate sensory processes, such as contrast sensitivity (Carrasco, 2009; Liu, Abrams, & Carrasco, 2009), spatial frequency (Abrams, Barbot, & Carrasco, 2010; Gobell & Carrasco, 2005), and lightness illusions (Economou, 2011; Tse, 2005), as well as size perception (Anton-Erxleben, Henrich, & Treue, 2007; Gobell & Carrasco, 2005).

In order to test whether the mechanisms underlying size adaptation are amenable to top-down modulation, the current study was designed to induce different size adaptation effects despite identical visual input. To this end, size adaptation was induced by directing attention to one of two sets of objects present in one adaptation display: One set of symbols formed a square larger and the other set of symbols formed a square smaller than the subsequently presented target.

We hypothesized that focusing on the outer or inner symbols would cause them to be perceived as one object, either by inducing imaginary lines between the four symbols or—as suggested by the Gestalt laws of grouping—by grouping them based on the law of similarity in color and form. In more detail, focusing on the inner symbols forming the smaller square should generate an object representation similar to that caused by a small adaptor. On the other hand, focusing on the symbols forming the larger square should cause an object representation similar to that caused by a large adapter. Conclusively, we expected differential size adaptation effects for the two attention conditions.

Methods

Participants

Sixteen subjects (eight women, mean age: 25.9 years, age range: 20–42) took part in the current study. All subjects were right-handed as measured using the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. Normal color vision in all subjects was assessed by pseudoisochromatic color plates (Velhagen & Broschmann, 2003). Prior to the experiment, written informed consent was obtained in accordance with the Declaration of Helsinki. The study was approved by the ethics committee of the German Society of Psychology, and participants were remunerated for their time.

Stimuli

Stimuli were presented on a 22-in. Samsung SyncMaster monitor (120 Hz) at a distance of 72 cm. Distance was preserved by a chin and forehead rest. Each trial consisted of two displays: 5 s of the adaptation display (Figure 1A through C) was followed by a 200-ms test display (Figure 1D). A fixation cross was present in the center of the screen throughout the entire experiment, i.e., also between trials (Figure 1E). The adaptation display contained two grids of white squares (9×9 squares of 0.6° arranged with a distance of 0.6° in between, making up a large square of $10.2° \times 10.2°$) shown at 5.6° eccentricity on a black background (Figure 1A). In all but the control condition, one of the two grids contained additionally eight symbols, replacing eight of the little white squares. These symbols always consisted of a set of four circles and a set of four triangles, and they formed the corners of a small (3.6°) and a large (8.1°) square within the grid (Figure 1B, C). To avoid afterimages, all symbols flickered at a frequency of 4 Hz from blue to its complementary color orange (circles) and from red to its complementary color cyan (triangles). Hence, the colors red/blue and cyan/orange were on the screen simultaneously. In order to rule out the possibility of salience differences between triangles and circles, i.e., inner and outer symbols, we ensured matched luminance values of these colors. The test display, which immediately followed the adaptation display, contained two squares, the test and the probe (Figure 1D). The test square of constant size (4.9°) was shown ipsilateral to the side on which the colored symbols were presented. The probe square varied in size (3.5°, 4°, 4.5°, 4.9°, 5.5°, 5.9°, 6.4°) and was shown opposite to the test square. The perceived size of the test square was estimated using the method of

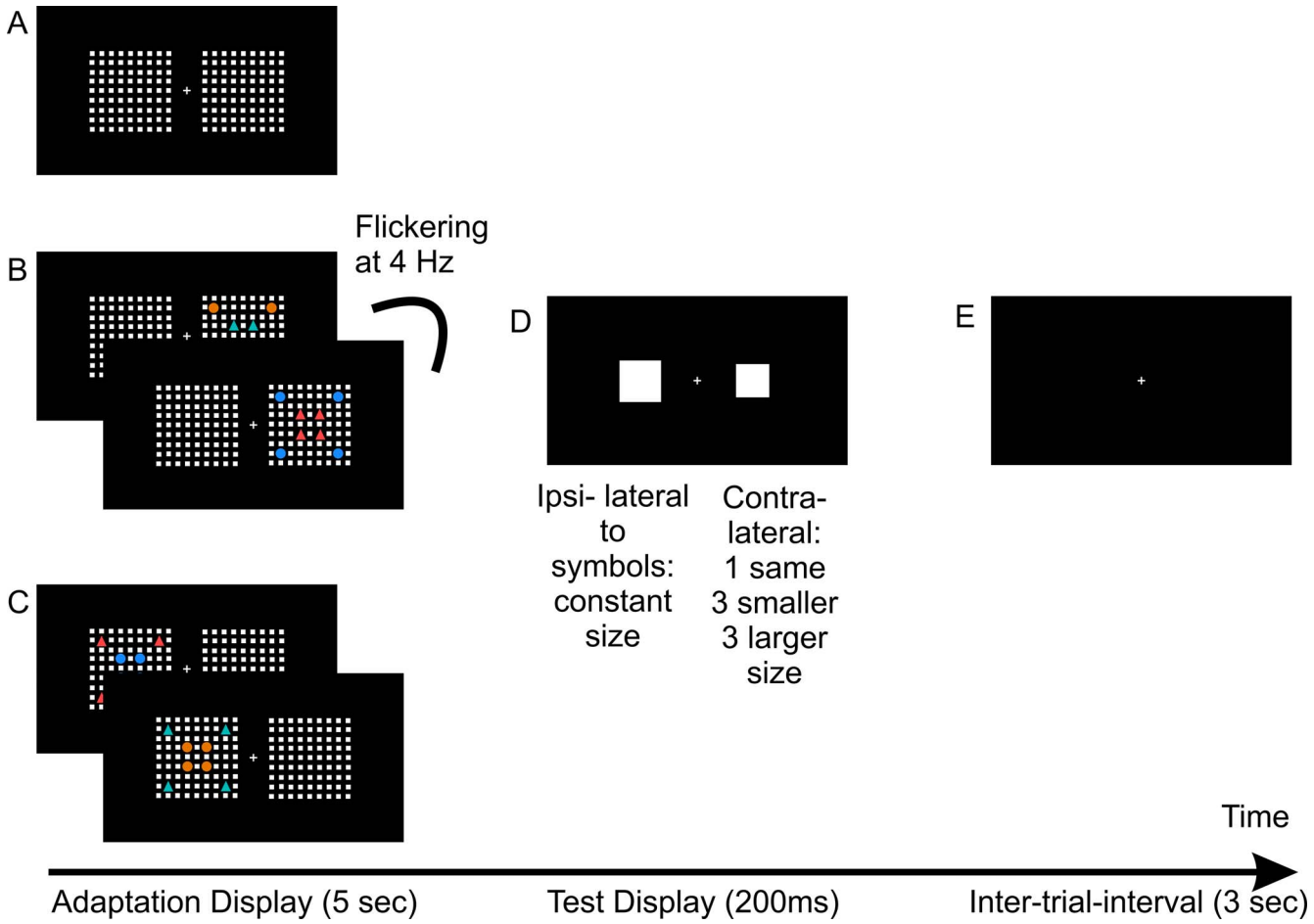

Figure 1. Illustration of the time course of a single trial. The adaptation display contained either no symbols in the control condition (A) or circles shown within triangles (B) or triangles within circles (C). Both appeared either on the right (B) or left (C) side of the screen and were in all cases followed by the test display (D) and the intertrial interval (E).

constant stimuli. Between trials, only the fixation cross remained on the screen for 3 s (Figure 1E).

Procedure

The experiment consisted of 280 trials, which were presented in 20 blocks (four control, eight small focus, eight large focus condition), each of which consisted of 14 trials (each of the seven comparison squares shown twice). The positions of symbols within the grid (circles within triangles, Figure 1B, or triangles within circles, Figure 1C) and between the grids (symbols in the left or right grid) were balanced across blocks. Subjects were instructed to detect a luminance change, which was randomly assigned to one of the four respective target symbols during the adaptation period (Figure 1A through C) and to indicate the larger square on the following test display (Figure 1D). The target symbols were indicated on the screen at the beginning of each block. For the large adapter condition, target symbols were the symbols forming the outer square in the grid ("outer circles" or "outer triangles"). For the small adapter condition, target symbols were those forming the inner square in the grid ("inner circles" or "inner triangles"). Luminance changes had to be reported as quickly and as accurately as possible using the left index finger. The larger square had to be indicated as quickly and as accurately as possible using the right index (to indicate the left square) and right middle (to indicate the right square) fingers.

Data analysis

Luminance detection in a trial was rated as accurate when subjects responded—using their left index finger—within 500 ms (two flickers) after the luminance change. For the size judgments, trials without a valid response (i.e., using their right index or middle finger) during the 3 s before the next trial started were defined as missing values ($M = 0.74\%$, $SD = 0.68\%$). Three subjects were excluded because their accuracy and missing values deviated more than 2 standard

deviations from the group's mean. On a single-subject basis, error trials, missing values, trials with response times (RTs) below 100 ms or differing more than 2 standard deviations from the group mean were excluded.

The point of subjective equality (PSE) for perceived size of the test square was estimated by fitting a logistic function to the responses using MATLAB 8.5 (The MathWorks Inc., Natick, MA) and the Palamedes Toolbox (Prins & Kingdom, 2009). The slope was fixed to 5.03, which was derived from estimating the mean slope of the whole group as suggested by Peng, Jaeger, and Hautus (2014). Goodness of fit was estimated using the implemented function in the Palamedes Toolbox based on Wichmann and Hill (2001). The number of simulations performed to determine the goodness of fit was equal to 400. The free statistical software R (R Foundation for Statistical Computing, Vienna, Austria; www.r-project.org) was used for subsequent statistical analysis of the goodness of fit and the extracted PSEs. Pairwise comparisons were performed for the control condition (no symbols), the small focus condition (luminance detection on symbols forming the smaller adapter), and the large focus condition (luminance detection on symbols forming the larger adapter). Moreover, in order to test for differences in difficulties between the conditions, inverse efficiency scores (IESs) were calculated by dividing the RTs of the small and large focus conditions by the respective accuracy in the luminance detection task (Bruyer & Brysbaert, 2011). The advantage of using IESs is that they account for potential speed–accuracy trade-offs. Better performance is described by lower IES values (Townsend & Ashby, 1983).

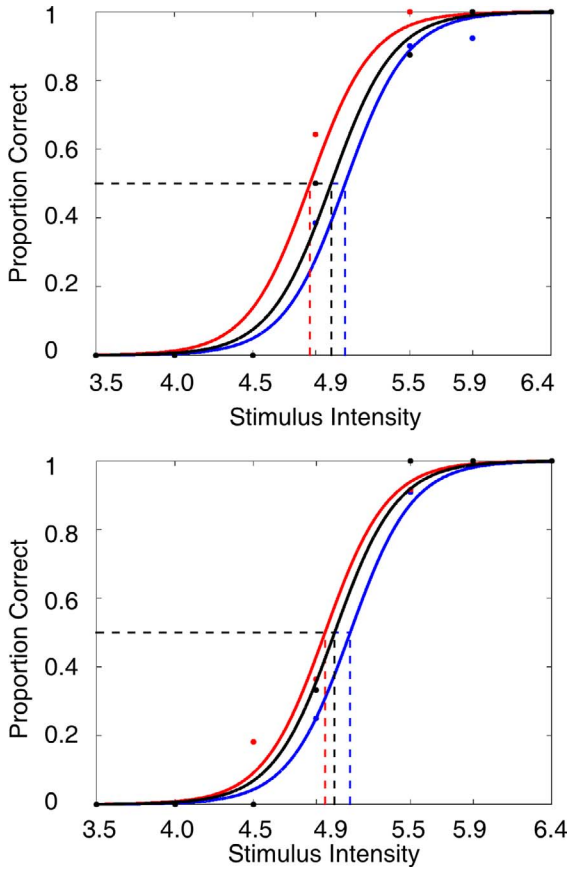

Figure 2. Exemplary psychometric functions of two subjects. The point of subjective equality (PSE) is estimated for the control condition (black curve) and the inner (blue curve) and the outer focus conditions (red curve) by fitting psychometric functions to the size judgments of the seven comparison squares (3.5°, 4°, 4.5°, 4.9°, 5.5°, 5.9°, 6.4°) with the slope fixed to the group slope of five. The dashed lines indicate the comparison size at which size judgment performance was at chance level and show the PSE for each condition. The shift to the right in the inner focus condition (blue curve) illustrates the increase in perceived size.

Results

Subjects missed, on average, 0.62% of the size judgments. Misses were trials during which no response was given until the start of the next trial, i.e., within an interval of 3 s. Participants had an accuracy of 94.23% on the luminance detection task as indicated by a button-press within 500 ms after appearance of the dot. When the focus was directed toward the inner symbols forming a square smaller than the target, subjects perceived the subsequently presented target, on average, as 3.16% larger (5.15°) than in the neutral condition (4.99°), and focusing on the four outer symbols forming a square larger than the target led to almost no change (4.97°) relative to the neutral condition. Exemplary psychometric functions of two subjects are plotted in Figure 2 and show the shift to the right for the inner focus as compared to the outer focus condition. This reflects an increase in perceived size. Pairwise comparisons using multiple paired two-sided t tests with p values adjusted by applying the Holm correction were performed (Figure 3). The results show that perceived size during the inner focus trials was significantly larger as compared to the outer focus, $t(1, 12) = 3.47$, $p = 0.014$, and to the control trials, $t(1, 12) = 2.59$, $p = 0.047$, and there was no significant change in perceived size for the outer focus trials as compared to control trials, $t(1, 12) = -0.38$, $p = 0.711$. The IES for the luminance detection task indicated that the absence of a decrease in perceived size for the large focus condition can be explained by difficulties keeping the focus widespread enough as indicated by the larger IES for the large

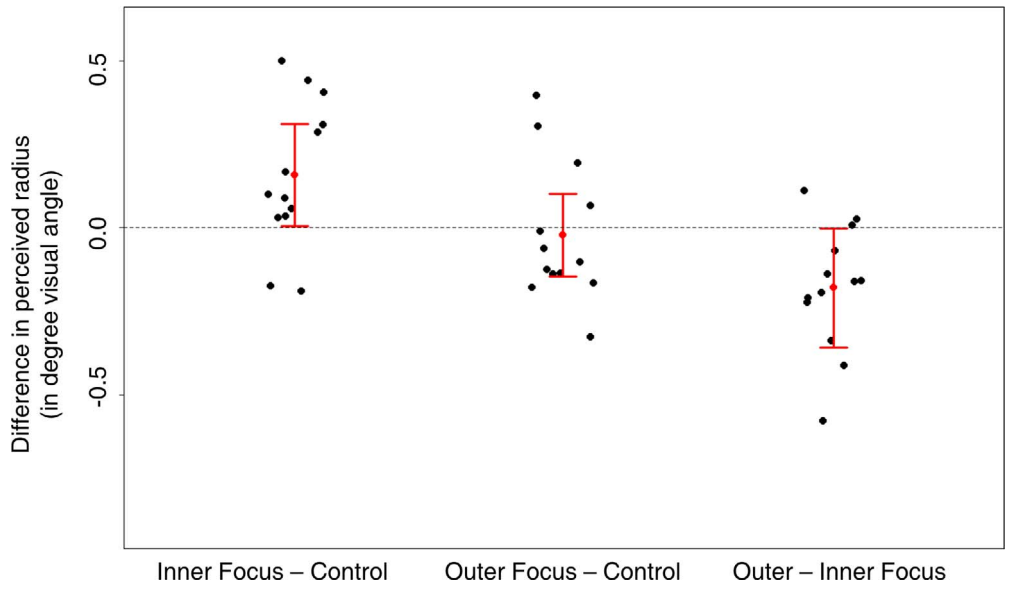

Figure 3. Pairwise comparisons for the three conditions. The individual differences in PSE (in degree of visual angle) are represented by the black dots. The red bars indicate the 95% confidence interval for each pairwise comparison. The dashed line indicates that there is no difference in perception.

focus trials ($M = 2.10$, $SD = 0.36$), which show that establishing the large focus was more difficult than establishing the small focus (IES $M = 1.86$, $SD = 0.35$), $t(1, 12) = -6.37$, $p < 0.01$.

Pairwise comparisons (Holm corrected) showed that the goodness of fit did not differ between conditions: small vs. large, $t(1, 12) = -0.96$, $p = 0.41$; small vs. neutral, $t(1, 12) = -2.07$, $p = 0.18$; neutral vs. large, $t(1, 12) = -1.34$, $p = 0.41$. However, although psychometric functions could be successfully fit for all subjects, the goodness of fit estimates indicate that for three subjects there was one condition with a bad fit ($p < 0.05$).[1]

Discussion

The current study investigated the influence of attention on size adaptation. In particular, it tested whether size adaptation can be induced on the basis of identical bottom-up information merely with different top-down settings. This approach helps to determine whether size adaptation involves early preattentive levels of visual processing or occurs later on during attentive processing stages, similar to what has been shown in other contexts, e.g., motion adaptation (Alais & Blake, 1999; Lankheet & Verstraten, 1995; Raymond, 2000). In order to investigate this, a single adaptation display was employed with bottom-up stimulation being constant across all conditions. However, when subjects had to focus on symbols forming an adapter smaller than the subsequently presented target, perceived target size was significantly increased as compared to control trials and trials during which subjects were instructed to focus on symbols forming a larger adapter.

Size distortions induced by the adapter displays used in the present experiment can arise either due to adaptation processes directly related to size representations or, alternatively, due to position effects induced by flickering. It has been demonstrated that flickering can affect space representations (Whitney, 2002; Yilmaz, Tripathy, Patel, & Ogmen, 2007). However, flickering in a bottom-up sense cannot account for altered size distortion as induced in the present experiment because displays were identical across conditions. In particular, both the attended as well as the unattended quadruples were flickering, and hence, any related space distortion should be the same in both conditions. Thus, a systematic effect is expected only when the position effects induced by flickering are modulated by attention. This could lead to local feature adaptation rather than adaptation to the large or small square they form collectively. The current study does not rule out this possibility. Anyway, both interpretations are consistent in terms of a role of attentional modulation of size adaptation.

In principle, the interaction with attention can affect size perception via two different mechanisms: On the one hand, spatial distortions induced by flickering may generate aftereffects that directly change the perceived size of the test stimulus. However, in order to account for the present data, this interpretation requires the assumption that the respective space distortions extend spatially because the flickering quadruples and the

corners of the test stimuli never spatially coincided. On the other hand, in the present experiment, flickering may change perceived size indirectly by altering the adapter stimulus. In particular, flickering could adjust the position of the (attended) quadruples, which, when perceptually grouped, form a square of modified size. This square could then induce size adaptation effects affecting the perceived size of a subsequent test stimulus. This view implies that the prolonged activation of a particular size representation leads to an adaptation and hence to a reduced response when perceiving the test stimulus. The effects of adaptation in visual perception have reliably been demonstrated in a variety of experiments (see Kohn, 2007, for a review). We therefore suggest that the attention-induced size changes observed in the present experiment involve adaptation mechanisms related to size representations. In addition, we conclude that size adaptation is amenable to top-down modulation.

Although the results show that identical physical displays can have very different effects on size perception, depending on different top-down settings, the findings were asymmetrical. The difference between the small and the large focus conditions was mainly driven by the size overestimation in the small focus condition. The absence of a change in size perception in the large focus condition could result from an inability to direct attention to the outer symbols forming the adapter. This is evidenced by a worse performance on the luminance detection task as compared to the small focus condition, suggesting that the elements forming the larger object were less efficiently selected. Apart from this, the lack of adaptation effects triggered by a large attentional focus could also arise from reduced spatial resolution at larger eccentricities due to a lesser extent of cortical magnification (Duncan & Boynton, 2003).

Another explanation for the absence of size adaptation in the large focus condition may be derived from the nature of attention selection. Although the experimental manipulation was object-based, i.e., binding the outer or inner symbols together, thereby forming a large or small adapter square, respectively, the resulting attention deployment may have been spatial in nature. Subjects may have solved the task by selectively increasing and decreasing the size of the attentional window. This would imply that in the large focus condition two adapters were processed in parallel, leading to a cancellation of over- and underestimation of size. Theoretically, such a cancellation could arise on different levels of processing. For instance, the symbols could be integrated before the initiation of the actual adaptation process. In this scenario, both sets of symbols would together form a neutral stimulus that does not initiate a particular adaptation bias. Alternatively, the two sets of symbols could simultaneously trigger two counteracting adaptation processes. However, this second explanation would only hold if two size adaptation effects initiated added up linearly. Evidence against a linear additivity of over- and underestimation in size adaptation stems, however, from a previous study that found larger changes in size perception for the underestimation versions (Kreutzer, Weidner, & Fink, 2015). Nevertheless, we cannot rule out the possibility that there is a nonlinear additive relationship between the over- and underestimation that could lead to cancellation of both effects in the current study. Future research needs to further investigate the nonlinearity of the attentional influence on size adaptation that was found for the small and the large focus in the current study.

Finally, it is also possible that the reason for the asymmetry of effects is more general. A bias to overestimate the size of the test stimulus relative to the comparison stimulus could arise due to its appearance on the attended side. Evidence in favor of this hypothesis stems from studies showing that transient attention increases perceived gap size (Gobell & Carrasco, 2005). In that case, the attended size would always be perceived larger than the unattended side, pushing the overestimation in the small focus condition and counteracting the underestimation in the large focus condition. The observed asymmetry in the current study could thus, at least partly, arise from a general size misperception caused by attending to one side.

Regardless of the reason for the larger adaptation effect during small focus trials, the present results clearly show that the effects of adapters on the subsequent target stimulus are not exclusively determined by the visual features of the adapter layout. Different effects were induced by identical features. Assuming a purely feed-forward mechanism underlying size adaptation, one and the same adaptation display should have triggered the same change in perceived size independent of the observer's attentional state. Thus, if size adaptation was purely stimulus dependent, no significant differences in the PSEs between the two experimental conditions were to be expected. However, we did observe a higher PSE for the small focus trials as compared to the control condition as well as compared to the large focus condition, which only differed with regard to the top-down settings established by the attentional instructions. The accessibility of top-down settings led us to conclude that size adaptation cannot exclusively be accounted for by bottom-up mechanisms per se. In other words, the involvement of attention rules out a pure feed-forward mechanism for size adaptation and strongly suggests iterative processing between lower and higher cortical regions allowing the integration of purely visual feed-forward and attentional feedback information. As suggested by Choui-

nard and Ivanowich (2014), this is also in line with MEG data showing that frontal lobe structures can process visual context information before feeding back into early visual areas (Bar et al., 2006). Similarly, attention may affect early representations of the adapter, potentially boosting the response to the inner versus the outer adapter, hence rendering these representations behaviorally relevant.

Studies investigating object-substitution masking suggest that visual perception arises from iterative exchanges between brain regions connected by two-way pathways (Di Lollo, 2014; Enns & Di Lollo, 2000), and V1 is most likely part of this iterative network. Evidence in favor of this assumption stems from both neurophysiological as well as functional imaging studies (e.g., Weidner, Shah, & Fink, 2006). For instance, it has been demonstrated that activation in V1 is modulated by feedback signals from higher visual areas (Lamme, Zipser, & Spekreijse, 1998). Furthermore, V1 has been demonstrated to be crucial for size perception (e.g., Murray et al., 2006; Schwarzkopf et al., 2011) as well as for attentional modulation (Fang et al., 2008). For instance, the effects of attention on lower visual areas have previously been described within the framework of the biased competition model, which assumes feedback from higher cortical regions (see Desimone, 1998, for a review). This view has been further substantiated by Noesselt et al. (2002), who reported evidence for attentional modulation of early visual processing via higher visual areas (V3/VP, V3a, and V4) and argued that V1 participates in selective processing of attended visual stimuli by means of delayed feedback from these areas. Taken together, these studies argue in favor of a bidirectional information processing system between V1 and higher visual areas. In line with these findings, top-down modulation of size adaptation observed in the present study suggests an involvement of abovementioned feedback mechanisms from higher cortical regions on V1 in order to generate size representations that become relevant for size adaptation.

It remains, however, unclear how exactly top-down modulation exerts its effects on size adaptation. The current findings suggest that size adaptation is not only based on low-level information, but rather involves fully integrated object representations. In the present experiment, these object representations are formed in a purely top-down fashion, binding individual elements to an integrated global percept, hence activating related size representations generating adaptation. This view implies that size adaptation originates in higher cortical regions presumably coding object features. Effects on low-level representation would then occur via back projections from higher to lower visual areas.

Alternatively, top-down modulation may act as a weighting mechanism that alters initial low-level representations (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995). In that case, top-down modulation may generate stronger and more robust variants of the initial representations that may enhance local contour interaction effects previously suggested to drive size adaptation effects (Pooresmaeili et al., 2013). In light of these previous studies, which were able to show that low-level stimuli per se can trigger size adaptation, the latter explanation is more likely. We therefore conclude that attention is able to weight the local processes proposed by Pooresmaeili et al. (2013) into one or the other direction, thereby either triggering overestimation (small focus) or no change in perceived size (large focus and control condition), depending on the attentional focus.

Conclusion

In sum, we observed that the same adapter display can lead to differential changes in size perception dependent upon the focus of attention. Data suggest that—similar to other sensory processes—rescaling perceived size after adaptation is not solely based upon feed-forward input to V1. Rather, the previously reported changes in V1—correlating with adaptation-induced changes in size perception (Pooresmaeili et al., 2013)—can be weighted by attention, thereby ruling out the possibility that size adaptation originates from local processes only.

Keywords: size perception, top-down modulation, object binding, visual illusions

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Footnote

[1] Excluding these subjects did not change the direction of our effect with subjects still perceiving the target larger in the small focus condition (5.05°) than in the large focus condition (4.94°). Yet, due to the decreased power when excluding another three subjects, this difference was only significant for uncorrected p values and showed trend-level significance after Holm correction, $t(1, 9) = 2.70$, $p = 0.02$, Holm-corrected $p = 0.07$.

References

Abrams, J., Barbot, A., & Carrasco, A. (2010). Voluntary attention increases perceived spatial frequency. *Attention, Perception, & Psychophysics, 72*(6), 1510–1521, doi:10.3758/APP.72.6.1510.

Alais, D., & Blake, R. (1999). Neural strength of visual attention gauged by motion adaptation. *Nature Neuroscience*, *2*(11), 1015–1018, doi:10.1038/14814.

Anton-Erxleben, K., Henrich, C., & Treue, S. (2007). Attention changes perceived size of moving visual patterns. *Journal of Vision*, *7*(11):5, 1–9, doi:10.1167/7.11.5. [PubMed] [Article]

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Schmidt, A. M., ... Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences, USA, 103*(2), 449–454, doi:10.1073/pnas.0507062103.

Bruyer, R., & Brysbaert, M. (2011). Combining speed and accuracy in cognitive psychology: Is the inverse efficiency score (IES) a better dependent variable than the mean reaction time (RT) and the percentage of errors (PE)? *Psychologica Belgica, 51*(1), 5, doi:10.5334/pb-51-1-5.

Carrasco, M. (2009). Cross-modal attention enhances perceived contrast. *Proceedings of the National Academy of Sciences, USA, 106*(52), 22039–22040, doi:10.1073/pnas.0913322107.

Chouinard, P. A., & Ivanowich, M. (2014). Is the primary visual cortex a center stage for the visual phenomenology of object size? *The Journal of Neuroscience, 34*(6), 2013–2014, doi:10.1523/JNEUROSCI.4902-13.2014.

Cohen, L. H., & Lindley, S. B. (1938). Studies in vibratory sensibility. *The American Journal of Psychology, 51*(1), 44, doi:10.2307/1416415.

Desimone, R. (1998). Visual attention mediated by biased competition in extrastriate visual cortex. *Philosophical Transactions of the Royal Society B: Biological Sciences, 353*(1373), 1245–1255, doi:10.1098/rstb.1998.0280.

Di Lollo, V. (2014). Reentrant processing mediates object substitution masking: Comment on Põder (2013). *Frontiers in Psychology, 5*, 819, doi:10.3389/fpsyg.2014.00819.

Dix, M. R., Hallpike, C. S., & Hood, J. D. (1949, Jul 9). Auditory adaptation in the human subject. *Nature, 164*, 59–60, doi:10.1038/164059b0.

Duncan, R. O., & Boynton, G. M. (2003). Cortical magnification within human primary visual cortex correlates with acuity thresholds. *Neuron, 38*(4), 659–671.

Economou, E. (2011). Attention affects the size of lightness illusions [Abstract]. *Perception*, *40*, 189.

Enns, J. T., & Di Lollo, V. (2000). What's new in visual masking? *Trends in Cognitive Sciences, 4*(9), 345–352, doi:10.1016/S1364-6613(00)01520-5.

Fang, F., Boyaci, H., Kersten, D., & Murray, S. O. (2008). Attention-dependent representation of a size illusion in human V1. *Current Biology, 18*(21), 1707–1712.

Found, A., & Müller, H. J. (1996). Searching for unknown feature targets on more than one dimension: Investigating a "dimension-weighting" account. *Perception & Psychophysics, 58*(1), 88–101, doi:10.3758/BF03205479.

Gobell, J., & Carrasco, M. (2005). Attention alters the appearance of spatial frequency and gap size. *Psychological Science, 16*(8), 644–651, doi:10.1111/j.1467-9280.2005.01588.x.

Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology, 97*(5), 3155–3164, doi:10.1152/jn.00086.2007.

Kreutzer, S., Weidner, R., & Fink, G. R. (2015). Rescaling retinal size into perceived size: Evidence for an occipital and parietal bottleneck. *Journal of Cognitive Neuroscience, 27*(7), 1334–1343, doi:10.1162/jocn_a_00784.

Lamme, V. A. F., Zipser, K., & Spekreijse, H. (1998). Figure-ground activity in primary visual cortex is suppressed by anesthesia. *Proceedings of the National Academy of Sciences, USA, 95*(6), 3263–3268.

Lankheet, M. J. M., & Verstraten, F. A. J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Research, 35*(10), 1401–1412, doi:10.1016/0042-6989(95)98720-T.

Liu, T., Abrams, J., & Carrasco, M. (2009). Voluntary attention enhances contrast appearance. *Psycho-*

logical Science, 20(3), 354–362, doi:10.1111/j.1467-9280.2009.02300.x.

Müller, H. J., Heller, D., & Ziegler, J. (1995). Visual search for singleton feature targets within and across feature dimensions. *Perception & Psychophysics, 57*(1), 1–17, doi:10.3758/BF03211845.

Murray, S. O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience, 9*(3), 429–434.

Noesselt, T., Hillyard, S. A., Woldorff, M. G., Schoenfeld, A., Hagner, T., Jäncke, L., & Heinze, H.-J. (2002). Delayed striate cortical activation during spatial attention. *Neuron, 35*(3), 575–587, doi:10.1016/S0896-6273(02)00781-X.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97–113.

O'Mara, S., Rowe, M. J., & Tarvin, R. P. (1988). Neural mechanisms in vibrotactile adaptation. *Journal of Neurophysiology, 59*(2), 607–622.

Peng, M., Jaeger, S. R., & Hautus, M. J. (2014). Fitting psychometric functions using a fixed-slope parameter: An advanced alternative for estimating odor thresholds with data generated by ASTM E679. *Chemical Senses, 39*(3), 229–241, doi:10.1093/chemse/bjt073.

Pooresmaeili, A., Arrighi, R., Biagi, L., & Morrone, M. C. (2013). Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. *The Journal of Neuroscience, 33*(40), 15999–16008, doi:10.1523/JNEUROSCI.1770-13.2013.

Prins, N., & Kingdom, F. A. A. (2009). *Palamedes: Matlab routines for analyzing psychophysical data.* Retrieved from www.palamedestoolbox.org.

Raymond, J. E. (2000). Attentional modulation of visual motion perception. *Trends in Cognitive Sciences, 4*(2), 42–50.

Schwarzkopf, D. S., Song, C., & Rees, G. (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14*(1), 28–30.

Sperandio, I., Chouinard, P. A., & Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience, 15*(4), 540–542.

Townsend, J. T., & Ashby, F. G. (1983). *Stochastic modeling of elementary psychological processes.* Cambridge, UK: Cambridge University Press.

Tse, P. U. (2005). Voluntary attention modulates the brightness of overlapping transparent surfaces. *Vision Research, 45*(9), 1095–1098, doi:10.1016/j.visres.2004.11.001.

Velhagen, K., & Broschmann, D. (2003). *Tafeln zur Prüfung des Farbensinnes* (33rd ed.) [Translation: *Pseudoisochromatic colour plates*]. Stuttgart: Thieme.

Weidner, R., Shah, N. J., & Fink, G. R. (2006). The neural basis of perceptual hypothesis generation and testing. *Journal of Cognitive Neuroscience, 18*(2), 258–266, doi:10.1162/jocn.2006.18.2.258.

Westerman, L. A., & Smith, R. L. (1984). Rapid and short-term adaptation in auditory nerve responses. *Hearing Research, 15*(3), 249–260, doi:10.1016/0378-5955(84)90032-7.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences, 6*(5), 211–216, doi:10.1016/S1364-6613(02)01887-9.

Wichmann, F. A., & Hill, N. J. (2001). The psychometric function: I. Fitting, sampling, and goodness of fit. *Perception & Psychophysics, 63*(8), 1293–1313, doi:10.3758/BF03194544.

Yilmaz, O., Tripathy, S. P., Patel, S. S., & Ogmen, H. (2007). Attraction of flashes to moving dots. *Vision Research, 47*(20), 2603–2615, doi:10.1016/j.visres.2007.06.017.